

Specificity and generalization of visual perceptual learning in humans: an event-related potential study

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To investigate the neural correlates of specificity and generalization of visual perceptual learning, we recorded event-related potentials from human adults when they were trained with a simple visual discrimination task. While reaction times decreased significantly across training sessions, event-related potentials showed larger P2 amplitudes (~210 ms) over the left occipital/parietal areas and smaller N1 amplitudes (~140 ms) at the left parietal site

with more practice. Similar to reaction times, the training effect on the P2 amplitudes was specific to stimulus orientation. However, the N1 effect was generalized over differently oriented stimuli. These results indicated the complexity of the neural substance underlying perceptual learning, relative to behavioral level. *NeuroReport* 14:587–590 © 2003 Lippincott Williams & Wilkins.

Key words: Event-related potentials (ERPs); Generalization; Human adults; Orientation; Perceptual learning; Specificity; Visual system

INTRODUCTION

Performance in a number of perceptual tasks improves as a result of training, not only during childhood, but also in adults [1]. In the human visual system, many behavioral studies have found that perceptual learning is specific to simple stimulus attributes (e.g. position, orientation) in various paradigms [2]. For instance, subjects' performance in a texture discrimination task of lines improved dramatically with practice. However, when the target and background lines were rotated 90°, the improvement did not transfer and the performance dropped back to the pre-training level [3]. Such stimulus specificity implies that perceptual learning might take place at relatively low-levels of the visual pathway where receptive fields retain fine selectivity for these simple attributes. A few neuroscientific studies have focused on investigation of stimulus-specific learning effects in the lower visual areas. For example, by recording ERP from the human occipital cortex, Skrandies *et al.* found that learning a vernier acuity task of vertical lines induced larger amplitudes and shorter latencies, which did not transfer to horizontal lines [4].

On the other hand, recent psychophysical studies argued that stimulus specificity does not hold all the time. For instance, learning transfers between stimuli when a task becomes easier [5]. Even for a difficult task, although there is no direct transfer, learning nevertheless accelerates [6]. These studies further indicate that generalization is also

common in perceptual learning [6]. Training subjects with one simple visual task might induce not only stimulus-specific effects but also generalized effects. However, neural studies of this issue are lacking. The neural correlates of specificity and generalization of visual perceptual learning remain unidentified.

In the present study, we recorded ERPs from human adults while they were being trained with a simple visual discrimination task. Two sets of stimuli, in which the line elements in one set were rotated 90° from those in the other, were used in the experiment. By observing the training effects on ERPs and examining whether these effects could transfer from one set of stimuli to the other, we investigated the neural correlates of specificity and generalization of visual perceptual learning.

MATERIALS AND METHODS

Subjects: Twelve college and graduate students (three females) participated in this experiment as paid volunteers. Subjects were 19–25 years old with normal or corrected-to-normal vision and were naive to the task. All except one were right-handed.

Stimulus: Two sets of stimuli (set 1 and set 2, each set including five patterns, as illustrated in Fig. 1) were used in the experiment. Each stimulus (5.6 × 5.6°) was composed of

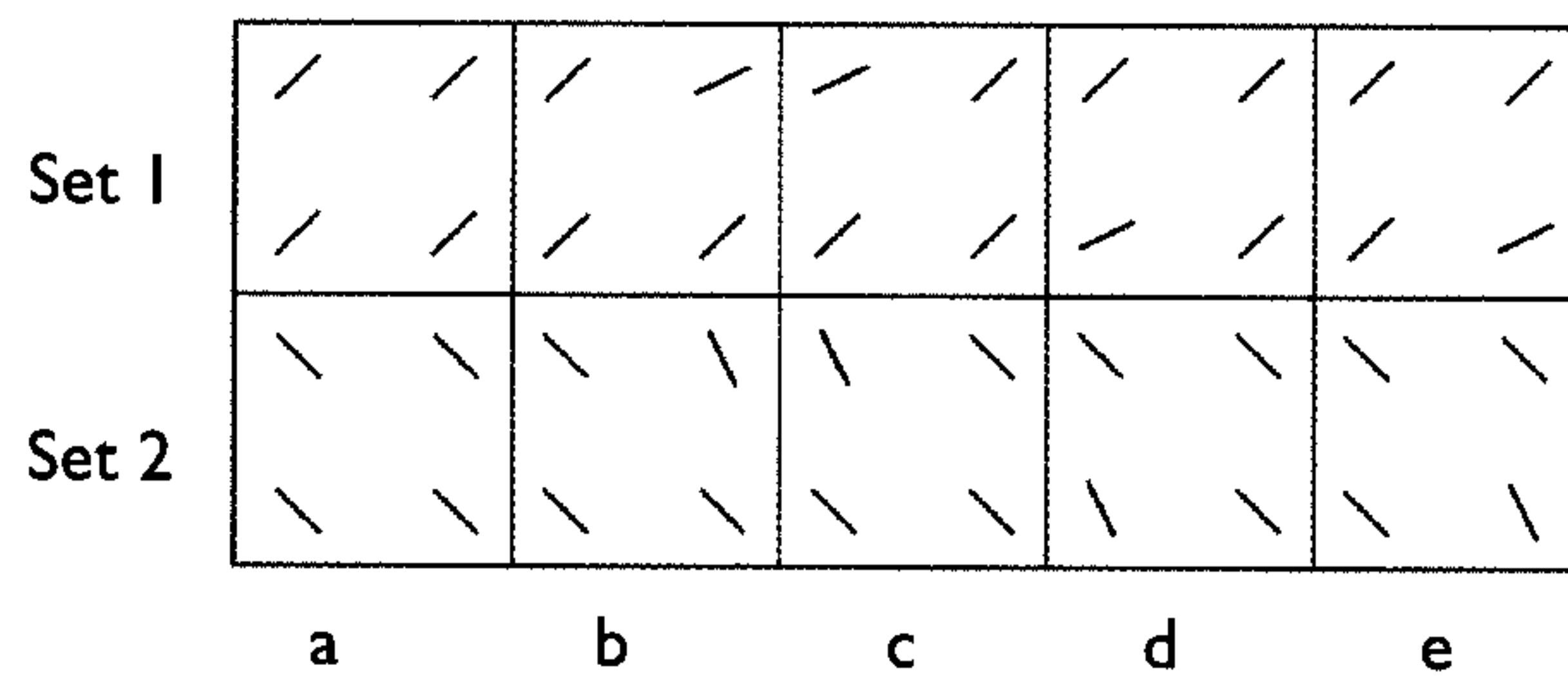


Fig. 1. Stimulus set 1 (top) and set 2 (bottom) used in the experiment. (a) target; (b–e) non-targets. The line elements were oriented at either 45° or 30° in set 1, and at either 135° or 120° in set 2. Six subjects were trained first with set 1 for two sessions, then with set 2 for two sessions, and the training sequence was reversed for the other six subjects.

four line elements (each 1.6° long and 0.1° wide) in a 2 × 2 array. In set 1 (Fig. 1, top), the four line elements had either an identical orientation of 45°, or the orientation of one line element was changed to 30°. In set 2 (Fig. 1, bottom), the line elements were rotated 90° from those of set 1 (i.e., the four line elements had either an identical orientation of 135°, or the orientation of one element was changed to 120°). All the stimuli were white on a uniform black background. Stimulus duration was 200 ms and interstimulus intervals (ISI) were randomized between 1400 and 1800 ms. At the center of the display, a green cross (0.3 × 0.3°) was present throughout as the fixation.

Procedure: The task was to discriminate whether the line elements in a stimulus had identical orientation or not. An oddball paradigm, as used in our previous study [7], was adopted. Subjects were instructed to press a button with their dominant hands when the targets (i.e. four line elements with identical orientation, Fig. 1a) were presented. Both accuracy and speed were emphasized. Subjects were first trained with one set of stimuli (initial stimuli) and then with the other set (rotated stimuli). For half the subjects initial stimuli were from stimulus set 1, and for the other half, set 2. Each set of stimuli was presented in two consecutive sessions (first session and second session). Thus, there were four training sessions in total for each subject. Each training session contained eight blocks of 50 trials. The target and the four types of non-targets were interspersed at random and with equal probability (20%) in a block. The experiment lasted about 2 h for each subject. At the beginning of the experiment, each subject practiced the operation for one or two blocks of initial stimuli to ensure that they understood the task. The data from the practice blocks was not used in the analysis.

EEG recording and analysis: Electroencephalogram (EEG) was recorded from electrodes at 17 standard sites of international 10/20 system (including F3, F4, F7, F8, C3, C4, T3, T4, P3, P4, T5, T6, O1, O2, Fz, Cz, Pz) and 11 additional sites (including FC3, FC4, FT7, FT8, CP3, CP4, TP7, TP8, CPz, Oz and right mastoid). Horizontal and vertical electro-oculograms (EOGs) were also recorded. EEG was physically referenced to the left mastoid and was then re-referenced off-line to the average of the left and right mastoid. Electrode impedance was kept below 5 kΩ. EEG

was amplified with a bandpass of 0.1–40 Hz, digitized on-line at a sampling rate of 250 Hz and a sampling resolution of 16 bits. Each epoch of EEG was from 200 ms pre-stimulus to 1000 ms post-stimulus. To minimize movement-related artifacts of finger response, ERPs to all non-targets (without explicit response) in each session were averaged. Trials contaminated by eye blinks, muscle potentials and other artifacts at any electrode, as well as trials with incorrect responses were excluded from averaging. The baseline for amplitude measurement was defined as the mean voltage of 200 ms pre-stimulus period.

Behavioral data were analyzed with repeated-measure ANOVAs with the two factors being training (first *vs* second session) and transfer (initial *vs* rotated stimuli). ERP peak amplitudes were measured from O1, O2, P3 and P4 sites, where ERPs showed obvious differences among sessions and then subjected to ANOVAs with the factors of training, transfer, area (occipital *vs* parietal area), and hemisphere (left *vs* right hemisphere).

RESULTS

Performance: Reaction times (RTs) were faster in the second session than in the first ($F(1,11) = 14.212, p < 0.004$). However, both the main effect of transfer ($p > 0.2$) and the interaction of transfer × training ($p > 0.2$) were not significant, suggesting that the training effect on reaction times did not transfer from initial stimuli to rotated stimuli (Fig. 2). Response accuracy was high and stable (averaged 98.5%) throughout the experiment.

ERPs: All the ERPs were characterized by P1 (70–120 ms), N1 (120–170 ms), P2 (180–240 ms) and N2 (240–340 ms, with two small peaks at 260 and 310 ms) over the occipital-temporal and parietal areas; P190 (150–230 ms), N300 (270–330 ms) over the central/frontal areas (with the maximum at the frontal area); and a broadly distributed P3 (350–580 ms). Peak latencies of each component were similar for all training sessions. There were however, significant differences of ERP amplitude on two important components, i.e. N1 and P2, over posterior areas (Fig. 3).

P2 amplitudes: A significant training × hemisphere interaction ($F(1,11) = 11.229, p < 0.007$) was found on P2 amplitudes over the posterior areas. Further simple effects tests revealed that at the left occipital and parietal sites, the P2 was larger in the second session than in the first ($F(1,11) = 10.681, p < 0.008$), whereas at the right occipital and parietal sites, no significant training effect on the P2 amplitudes was found ($p > 0.2$). However, there was neither a significant main effect of transfer ($p > 0.6$) nor significant interactions between transfer and other factors (transfer × training: $p > 0.8$; transfer × hemisphere: $p > 0.3$), indicating that, the training effect on the P2 amplitudes did not transfer from initial stimuli to rotated stimuli (Figs. 2 and 3).

N1 amplitudes: There was a significant interaction of training × area × hemisphere ($F(1,11) = 9.922, p < 0.01$). Simple effects tests revealed that while there was no significant difference in N1 amplitudes between the first and second sessions at O1, O2 and P4 sites (all $p > 0.1$), the N1 was smaller in the second session than in the first session at

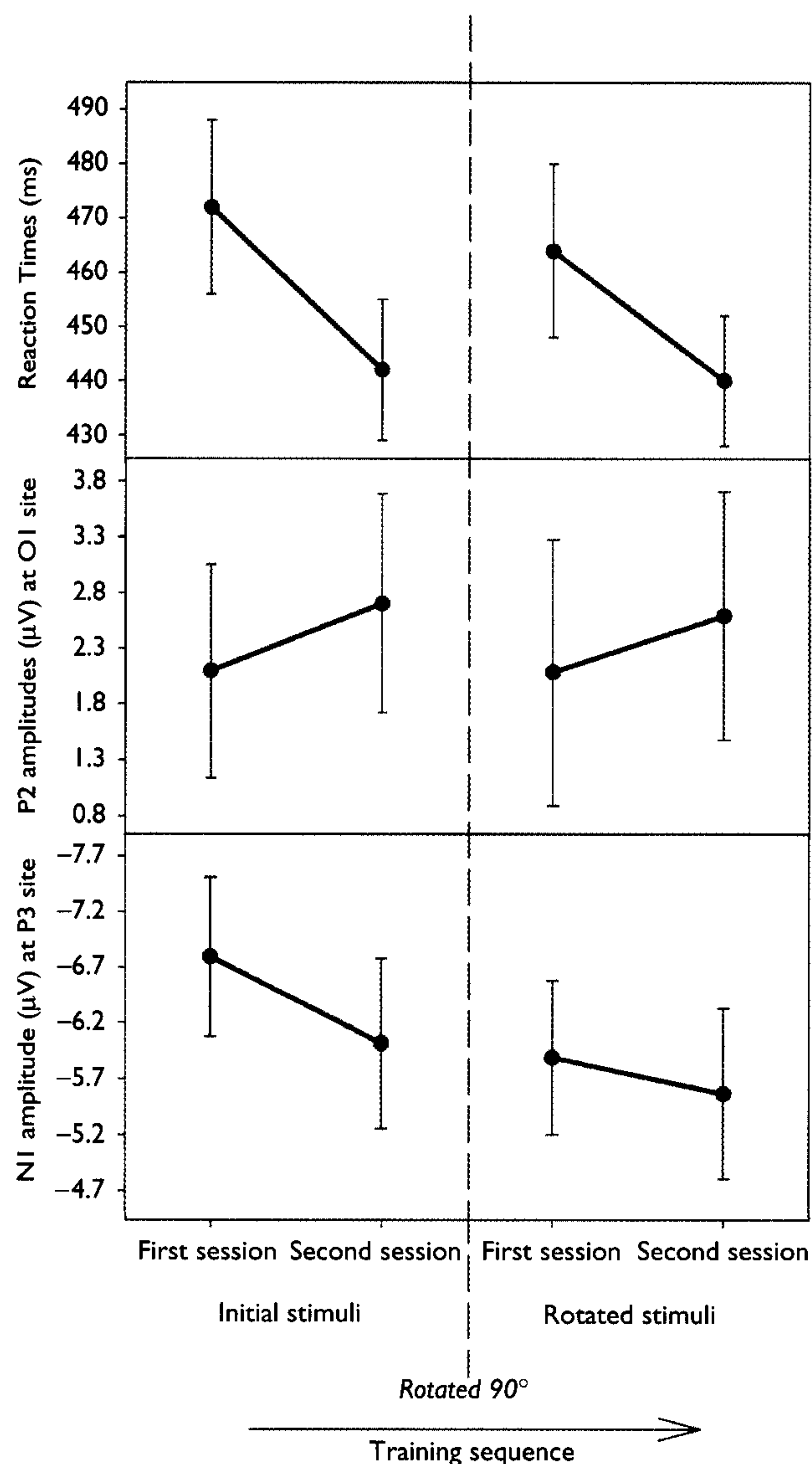


Fig. 2. Influence of training on reaction times (for target) and ERPs (for non-targets). The mean value (s.e.) of 12 subjects is presented. Reaction times were shortened significantly by training and this increase in performance was specific to stimulus orientation. For ERPs, training induced larger P2 amplitudes over left occipital/parietal areas and smaller N1 amplitudes at left parietal site. The effect on P2 amplitudes was orientation-specific, while the effect on N1 amplitudes could be generalized over different stimulus orientations.

the P3 site ($F(1,11) = 7.248$, $p < 0.022$). The interaction of transfer \times area \times hemisphere was also significant ($F(1,11) = 7.181$, $p < 0.022$). Furthermore, the N1 amplitudes at the P3 site were smaller for rotated stimuli than for initial stimuli (simple effect of transfer: $F(1,11) = 5.970$, $p < 0.034$). This result suggested that the training effect on N1 amplitudes at the left parietal site transferred from initial stimuli to rotated stimuli (Figs 2 and 3).

DISCUSSION

Consistent with previous behavioral observations that orientation-specific learning takes place in perceptual tasks

[3,8–10], training significantly shortened reaction times of our subjects in a simple visual task, and this improvement of performance did not transfer between different stimulus orientations.

At the same time, training induced P2 enhancement at occipital and parietal sites, which was specific to stimulus orientation. In a previous ERP study by Skrandies *et al.* [4], such a specific increment of amplitudes was also found over similar brain areas (posterior areas) and at a similar time interval (200–300 ms). In our experiment, the effect on the P2 amplitudes was paralleled by the effect on RTs. Since P2 has been found to be sensitive to stimulus orientation [11], the training-induced increase of P2 amplitudes might reflect a specific and efficient increase in neuronal sensitivity to the trained orientation, and it might be partially related to the electrophysiological substrates underlying the learning effect observed in RTs.

In addition, our orientation-specific effect on P2 was found mainly at the left posterior sites. Studies have shown that neurons at lower levels of the visual pathway are highly specialized for orientation, position, size, etc, whereas neurons in higher anatomical visual areas generalize over these simple stimulus attributes [12], as well as that the hemispheric asymmetry is more likely to occur at higher levels rather than at the low level of visual cortical processing [13]. Thus, it is plausible that the P2 effect might reflect neuronal plasticity in the intermediate visual cortex where both orientation selective units [12,14] and hemispheric asymmetry [15] have been found during visual processing. The related view that perceptual learning involves the intermediate cortical levels of visual processing, such as V2 or up to V4, has previously been proposed in a psychophysical study [16]. As more direct evidence of this view, recent brain imaging and single unit studies found significant orientation-specific learning effects in human V2, V3 [17] and monkey V4 [18].

Unlike the orientation-specific P2 effect, training had a generalized effect on the N1 amplitudes. That is, the N1 effect transferred between stimulus orientations while the P2 effect didn't. In addition, the distribution of these two effects showed some difference. While the P2 effect was observed at both the O1 and the P3 sites, the N1 effect was found only at the P3 site. These differences suggest that the observed N1 and P2 effects may reflect two different neuronal processes rather than a single process involved in learning of the present task. The N1 effect might indicate generalized perceptual learning in this task, which further supports that 'generalization is common in perceptual learning' proposed by Liu ([6]; also see the Introduction).

It's even more interesting that the present generalized effect on N1 (around 140 ms) appeared temporally earlier than the specific effect on P2 (around 210 ms). The Reverse Hierarchy Theory [5,19] that perceptual learning proceeds as a countercurrent along the cortical hierarchy might provide a possible explanation for this phenomenon. That is, learning begins at high generalizing levels of the visual pathway, which is followed by specific learning in low anatomical visual areas. Thus, the present finding that generalized learning occurs before specific learning investigated by ERPs might provide an illustration for the temporal relationship between specific and generalized perceptual learning proposed by the Reverse Hierarchy

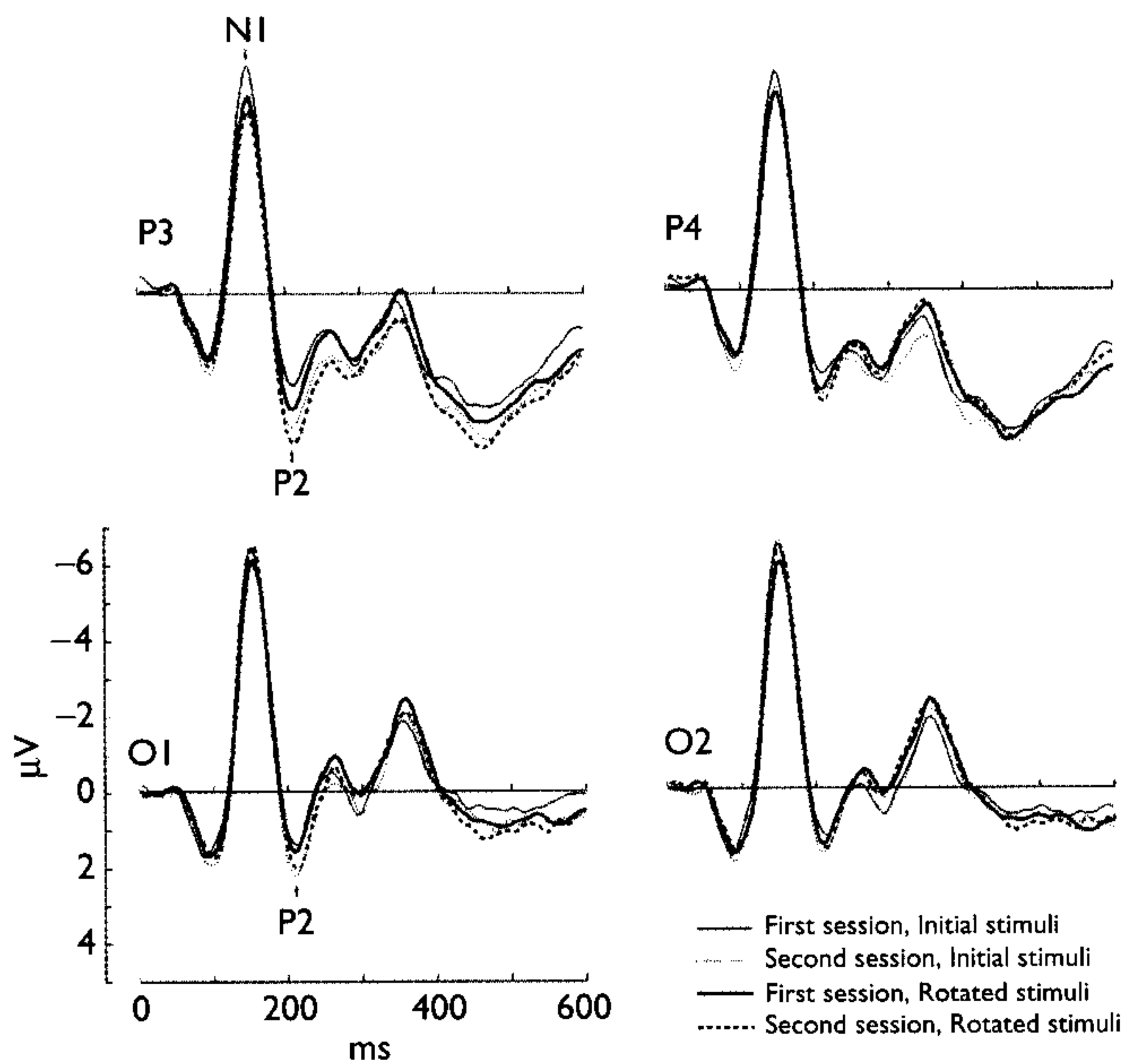


Fig. 3. Grand average ERPs ($n = 12$) for non-targets. Since for half the subjects initial stimuli were stimulus set 1 and rotated stimuli were set 2 and for the others initial stimuli were set 2 and rotated stimuli were set 1, the difference between the grand average ERP waveforms of initial and rotated stimuli might reflect the transferred training effect rather than physical stimulus parameters.

Theory. Alternatively, many studies found that the N1 amplitudes could be modulated by attention [20] and decreased attention might result in decreased neuronal responses [21]. It has been proposed that there is a strong interaction between attention and perceptual learning [22] and that 'diminished attentional modulation is a component of the learning process' [17]. Therefore, the possibility that the early decrement of the N1 amplitude might be related to a reduction in attentional modulation could not be excluded. Further studies are required to give an accurate assessment of the exact neural mechanisms of the N1 effect.

CONCLUSION

Our results illustrated that training the subjects to do a simple visual task within brief time periods could induce significant effects in both behavioral performance and brain activities. While behavioral results showed typical orientation-specific learning effects on RTs, ERPs revealed not only specific effects but also generalized effects. Moreover, some brain activity related to the generalized learning effects appeared temporally even earlier than some activity related to the specific effects. These results on specificity and generalization indicate the complexity of the neural substance underlying perceptual learning, relative to the behavioral level.

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